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GENETIC AND DEMOGRAPHIC CRITERIA FOR DEFINING POPULATION UNITS FOR CONSERVATION: THE VALUE OF CLEAR MESSAGES

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Abstract. In a recent paper on Harlequin Duck (*Histrionicus histrionicus*) interannual site fidelity (Iverson et al. 2004), we concluded that wintering populations were demographically structured at a finer geographic scale than that at which genetic differentiation was observed and that conservation efforts should recognize this degree of demographic independence. In a critique of our study, Pearce and Talbot (2006) contend that our measures of fidelity were not robust and imply that in the face of "mixed messages" we failed to appreciate the role of genetic data in defining population units. We recognize, as we did in our original paper, that our methods for quantifying site fidelity have some limitations; however, the patterns in our data are consistent with a considerable body of literature indicating high winter site fidelity in Harlequin Ducks. Moreover, we do not consider differences in the scales at which genetic and demographic structure are expressed to be "mixed messages," given the different spatial and temporal scales at which genetic and contemporary demographic processes operate. We emphasize that a lack of genetic differentiation does not necessarily preclude the existence of contemporary demographic structure with relevance for conservation.

Key words: demography, genetics, Harlequin Duck, Histrionicus histrionicus*, population structure, site fidelity.*

Criterios Demográficos y Genéticos para Definir Unidades Poblacionales para Conservación: el Valor de un Mensaje Claro

Resumen. En una publicación reciente sobre fidelidad internanual al sitio por parte de *Histrionicus histrionicus* (Iverson et al. 2004), concluimos que las poblaciones de invierno se encontraban estructuradas demográficamente a una escala geográfica menor que a la que se observa diferenciación genética, y que los esfuerzos puestos en conservación deberían considerar este grado de independencia demográfica. En una crítica a nuestro estudio, Pearce y Talbot (2006) argumentan que nuestras medidas de fidelidad no fueron robustas, implicando que, enfrentados a "mensajes mixtos", nosotros no apreciamos el papel de los datos genéticos en definir unidades poblacionales. Como lo hicimos en nuestra primera publicación, reconocemos que nuestros métodos para cuantificar la fidelidad al sitio tienen algunas limitaciones, pero los patrones en nuestros datos concuerdan con una vasta literatura que indica una alta fidelidad al sitio de invierno en *H. histrionicus*. Además, no consideramos que las diferencias en las escalas a las cuales se expresan las estructuras genéticas y demográficas sean "mensajes mixtos", dadas las diferentes escalas a las que operan los procesos genéticos y demográficos. Enfatizamos que la falta de diferenciación genética no excluye la existencia de estructura demográfica contemporánea que puede tener relevancia para la conservación.

Population management is clearly enhanced by knowledge of the demographic structure of animal populations, i.e., the scale at which changes in numbers of animals in one area are largely independent of changes occurring in another area. Quantifying the rate and scale of movements among putative population subunits is critical for this understanding (Walters 2000, Clark et al. 2004). In simple terms, in situations where animals move frequently and far, population dynamics are affected by immigration and emigration at relatively large geographic scales. Conversely, for animals that show strong site fidelity, population dynamics at relatively small scales are driven primarily by the intrinsic demographic properties of survival and productivity, i.e., they are demographically independent from other areas. Understanding the degree and scale of demographic independence is critical for identification of appropriate population subunits for conservation. Definition of appropriate management units is difficult (Dizon et al. 1992, Moritz 1994), particularly when applied to migratory animals (Esler 2000, Webster et al. 2002).

We (Iverson et al. 2004) conducted a study of winter site fidelity of Harlequin Ducks (*Histrionicus histrionicus*) in Prince William Sound, Alaska to evaluate the degree and scale of interannual dispersal and consider the subsequent conservation implications. We found high homing rates (>90%) to nonbreeding sites at a scale of kilometers to tens of kilometers and concluded that demographically independent population subunits exist at relatively small scales. Further, we noted that the scale of demographic independence indicated by our data was much smaller than the scale at which genetic differentiation was observed (Lanctot et al. 1999), and that genetic panmixia does not necessarily imply nonexistence of relevant demographic population structuring.

Pearce and Talbot (2006) have two primary criticisms of our paper (Iverson et al. 2004). First,

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they suggest our approach may not have adequately measured site fidelity. Second, they consider mechanisms by which the observed ''mixed message'' (different patterns and scales of genetic versus demographic population structuring) may have arisen, and imply that we did not fully appreciate the value derived from considering multiple markers when evaluating population structure. We address their criticisms below, primarily in relation to the latter concern, as we feel this issue has broad relevance for wildlife conservation.

DEFINING RELEVANT CONSERVATION UNITS

Good science starts with a clear definition of the question being asked. Confusion expressed over definition of population subunits for conservation, as well as the appropriateness of tools that can be used to evaluate population structure, may have arisen from imprecise questions. Specifically, managers and researchers need to communicate the spatial and temporal scales over which they wish to quantify population structure, as well as the underlying mechanisms and patterns that they wish to describe.

Some conservation efforts are explicitly concerned with preservation of genetic diversity; this is particularly true in cases where populations are extremely small or where population subunits are highly isolated (Lande 1988). However, we argue that the majority of wildlife conservation issues are concerned with understanding changes in animal numbers, across a range of spatial scales, at time frames measured in years to decades. In other words, the issues are primarily demographic and contemporary in nature. Under this scenario, we contend that conservation units are most appropriately defined by identifying the scale at which population dynamics of putative subunits are demographically independent.

There are many methods for inferring the degree of contemporary demographic independence among areas, each with associated advantages and shortcomings. Genetic data have been used for many taxa; advantages of this approach include the opportunity to gather samples across broad geographic scales, and the ease of sample processing and analysis relative to large-scale mark-recapture programs. However, one limitation of genetic data is that the patterns observed are the product of both historical and contemporary population processes. As such, one cannot necessarily infer patterns of contemporary demographic isolation from patterns in genetic data. This lack of a one-to-one relationship between contemporary demographic structure and genetic structure has often been treated as a ''mixed message'' with unclear interpretation.

We appreciate that there is considerable scientific interest in population structure beyond definition of appropriate population subunits for conservation, and that the field of population genetics encompasses a broad suite of interesting and important questions. However, our specific interest, as stated in our original paper, was to consider the conservation implications of observed levels of demographic independence, and to contrast our findings with inferences one might be tempted to draw from existing genetic data (Lanctot et al. 1999). For that particular purpose, we believe there is common misunderstanding of the inferences one can draw from different data types, which could be interpreted as ''mixed messages'' without a full appreciation of the spatial and temporal scales at which different markers indicate population structure.

IS HARLEQUIN DUCK WINTER SITE FIDELITY HIGH?

We measured homing rates of molting Harlequin Ducks, defined as the proportion of marked ducks that were recaptured at their original capture site, and used the results to infer the degree of interannual fidelity to nonbreeding sites. We found that over 90% of recaptured individuals were in the same locations as their original captures and that detected movements were on the scale of kilometers to tens of kilometers. From these findings, we concluded that site fidelity was high, with implications for the scale of demographic independence among nonbreeding population units. We recognize that our measure of homing rate has limitations and assumptions and explicitly acknowledged these in our original paper.

Pearce and Talbot (2006) correctly indicated that our measure of homing rate would be an overestimate of site fidelity if recapture efforts were lower in areas outside the primary study area. To evaluate whether this was likely to have strong influences on our estimates, we conducted captures at numerous supplementary sites that held concentrations of molting Harlequin Ducks and represented a range of distances (8–62 km) from the primary study area. Although we did not sample at every possible location within this range, none of the birds marked at the primary study site were captured at supplementary sites; we suggest this result would be very unlikely if there were demographically relevant movements from our primary study site at this scale. We also acknowledge that dispersal beyond a 62 km radius from our primary study site was possible; however, given the lack of evidence for movement at smaller scales, we suspect that demographically relevant movement at larger scales was unlikely.

Our findings and conclusions are corroborated by several studies on Harlequin Duck dispersal and site fidelity (Breault and Savard 1999, Robertson et al. 1999, 2000, Cooke et al. 2000, Iverson and Esler 2006). Collectively, these studies provide a strong basis for concluding that intra- and interannual fidelity to nonbreeding sites is quite high, and that this degree of site fidelity likely leads to demographic independence among nonbreeding sites at relatively small scales.

Pearce and Talbot (2006) suggested that, because our data were collected on adult Harlequin Ducks, high levels of juvenile dispersal might increase the scale of demographic independence and therefore might explain the ''mixed message'' observed between genetic and demographic population structure. However, the available data do not indicate this is the case. Regehr et al. (2001) found that at least some

juvenile Harlequin Ducks accompany their mothers to her wintering area, and Regehr (2003) further discovered that juvenile dispersal during the first winter was on a scale of only tens of kilometers. Also, Iverson and Esler (2006) found that intra-annual winter site fidelity was similar among all age cohorts of females tracked by radio-telemetry. Finally, juveniles constitute a small portion of the overall Harlequin Duck population; therefore, movement patterns of adults have a highly disproportionate effect on the degree of demographic independence.

We do not dispute that some dispersal of adult and juvenile Harlequin Ducks occurs; in fact, we have documented this at a range of spatial scales (Iverson et al. 2004, Iverson and Esler 2006). However, we have suggested (Iverson et al. 2004) and quantitatively demonstrated (Iverson and Esler 2006) that the observed rates of movement are low and lead to demographic independence of wintering aggregations at relatively small spatial scales. We agree with Pearce and Talbot (2006) that dispersal may lead to homogenization of gene frequencies observed at regional scales (Lanctot et al. 1999); however, this absolutely does not preclude the possibility that populations are structured demographically at much smaller scales.

In addition, we disagree with Pearce and Talbot's (2006) assertion that high fidelity to nonbreeding sites would lead to demographic and genetic structure only if nonbreeding population units remained as distinct units during the rest of the annual cycle. A number of mechanisms could maintain genetic distinctiveness even when different population units co-occur (e.g., assortative mating, pair formation at a different annual stage). More important for this discussion is that demographic independence can be relevant for conservation at any stage of the annual cycle. Our conservation concerns were framed as an issue on nonbreeding areas, and therefore it does not matter whether Harlequin Ducks from demographically distinct wintering areas co-occur during the breeding season. As long as inter- and intra-annual winter site fidelity are high, numerical trends of nonbreeding subunits will be driven by intrinsic survival rates, without opportunity for demographic rescue through dispersal from other subunits.

HARLEQUIN DUCK POPULATION UNITS FOR CONSERVATION

Pearce and Talbot (2006) recognize that genetic and demographic population structure are expressed at different spatial and temporal scales. However, rather than acknowledging that this may explain the "mixed message" observed for Harlequin Ducks, they seem to suggest that methodological problems with our demographic data are the cause. Our data, and those in the accumulated literature on nonbreeding site fidelity of Harlequin Ducks, strongly support the existence of demographic structuring at much smaller spatial scales than those at which genetic structure exists. We see this neither as conflicting data nor as a mixed message, but rather as a reasonable outcome of measurements of processes that occur at different spatial and temporal scales.

These are not merely academic issues, but have important implications for wildlife conservation. Our study site included areas affected by the 1989 *Exxon Valdez* oil spill and Harlequin Ducks were one of the species showing delayed recovery (Esler et al. 2002). Understanding the geographic scale at which putative subpopulations are demographically linked by dispersal allows clearer insights into the constraints on population recovery. We have determined (Iverson et al. 2004, Iverson and Esler 2006) that rates of Harlequin Duck movement between oiled and unoiled areas of Prince William Sound are low, thus the contribution of immigration to population recovery in oiled areas will be correspondingly low. Therefore, to be effective, management and restoration activities to ameliorate effects of the oil spill will need to be targeted to the specific areas and population subunits in the oil spill zone. To reiterate, this population management issue for Harlequin Ducks, like most wildlife conservation problems, is concerned with population dynamics at a contemporary time scale and, as such, requires a clear understanding of contemporary demographic population structure.

INTERPRETING "MIXED MESSAGES"

Our primary message in our original paper and this reply is that researchers and managers should not necessarily expect genetic population structure and contemporary demographic structure to show similar patterns. We want to be clear that we are *not* saying that genetic data are useless for inferring contemporary demographic population structure. In fact, they could be quite valuable; if genetic data indicate structure at a given scale, then there is certainly demographic structure at that scale. Genetics may be a particularly efficient way of evaluating demographic structure at a scale that may be of interest to managers. However, if no genetic structure is evident, one cannot infer that there is demographic panmixia at the same scale. In other words, lack of genetic structure does not provide any indication whether population subunits are demographically discrete at the contemporary time scale at which population management generally operates. We agree with Pearce and Talbot (2006) that consideration of more than one type of marker can lead to additional insights into questions of interest. We simply caution that genetic and demographic data should not be expected to necessarily lead to the same inferences about population structure relevant for conservation. We hope this exchange leads to critical thinking and additional research on the topic.

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ERRATUM

In Condor 107/4 (November 2005), the paper "Simultaneous multiple clutches and female breeding success in Mountain Quail," by Jeffrey L. Beck et al., contained several miscalculations by the authors. The Results on p. 893, second paragraph, second sentence should read (corrections highlighted in boldface): "Of these eggs, **391** (**64%**) hatched." and the last sentence should read "**Forty-four** of **435** eggs (**10%**) in successful nests did not hatch." On p. 894, in the last paragraph of the Results, sentences 3–5 should read "Total egg production for paired females was 284 eggs with **208** (**73%**) hatching. Of the hatched eggs, males hatched **53%** and females hatched **47%**. All 12 females hatched an average of **17** chicks (range: 8–**24**) from both clutches…" In addition, in the final paragraph of the discussion, the citation for the (USDI Federal Register 2003) should have been for the (**USDI Fish and Wildlife Service 2003**). The authors regret these errors.